Integral projection model (IPM): why, how and what for?

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Further Reading

Easterling, M., Ellner, S.P. and P.M. Dixon. 2000. Size-specific sensitivity: applying a new structured population model. *Ecology* 81, 694-708

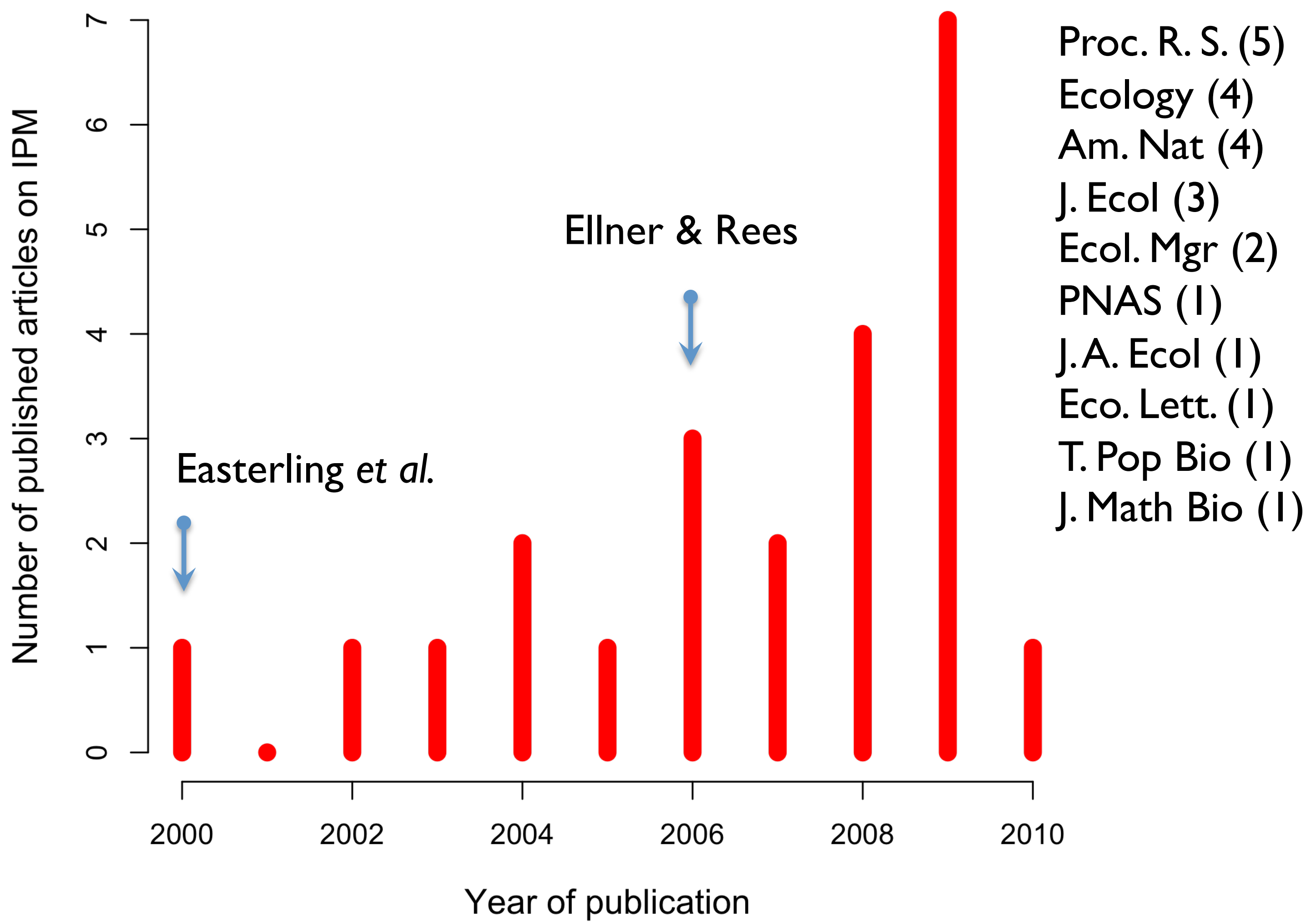
Ellner, S.P. and M. Rees 2006. Integral projection models for species with complex demography. *American Naturalist* 167, 410–28.

Ellner, S.P. and M. Rees 2007. Stochastic stable population growth in integral projection models: theory and application. *Journal of Mathematical Biology,* 54:227–256

First decade of IPM:

from Easterling *et al.* (2000) to Zuidema *et al.* (2010)

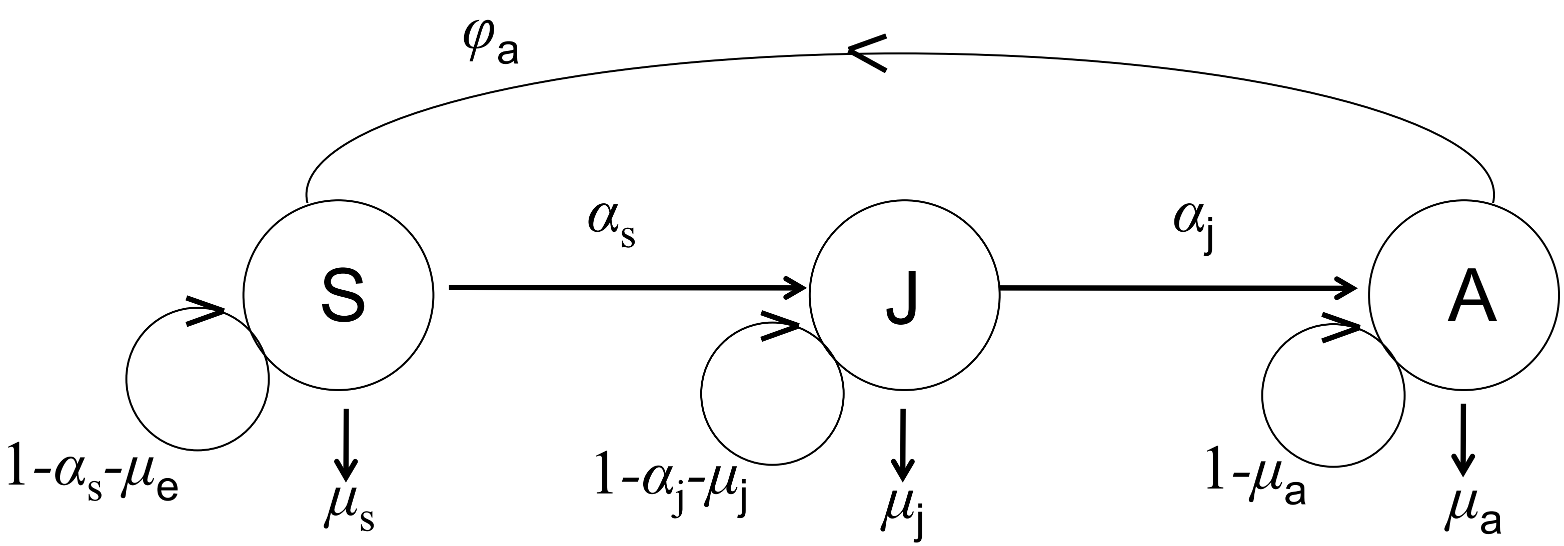
~23 articles from 15 first authors



Why IPM rather than MPM?

- Matrix dimension: Moloney-Vandermeer algorithm or biological criteria or..,?
  - Small sample size: over(under)-estimation of matrix transition elements
  - Assumption of constant vital rates within each size-class: the bigger the class the less this is true!
- Flexibility to test effects of multiple continuous covariates on population dynamics

Matrix Population Model



$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

Integral Projection Model

$$n(t+1) = \mathbf{A}n(t)$$

$$\underbrace{n(y,t+1)}_{\text{pop vec at } t+1} = \int_\Omega \underbrace{K(y,x)}_{\textbf{KERNEL}} \underbrace{n(x,t)}_{\text{pop vec at } t} dx$$

$$n(y,t+1) = \int_\Omega \overbrace{[\underbrace{p(x,y)}_{\text{Survival - Growth}} + \underbrace{f(x,y)}_{\text{Fertility}}]} n(x,t)\,dx$$

Easterling *et al.* 2000

IPM (size-dependent) Functions

$$n(y,t+1) = \int_{\Omega} [p(x,y) + f(x,y)] n(x,t) dx$$

Survival – Growth function

$$p(x,y) = s(x) g(x,y)$$

Fertility function

$$f(x,y) = s(x) f_f(x) f_n(x) p_g p_e f_d(y)$$

Survival function $s(x)$

s(x) modeling the probability of survival at time t +1 as a logistic function of size x at t

$$\operatorname{logit}[s(x)] = \log\left[\frac{s(x)}{1 - s(x)}\right] = \boldsymbol{\beta}_1 + \boldsymbol{\beta}_2 x$$

$$s(x) = \frac{\exp(\boldsymbol{\beta}_1 + \boldsymbol{\beta}_2 x)}{1 + \exp(\boldsymbol{\beta}_1 + \boldsymbol{\beta}_2 x)}$$

`HOW TO IN R?: fit a generalized linear model '`**`glm(y~x, family=binomial)`**`', with a binomial error structure, a log link function in R to obtain the βs and write the s(x) function.`

Growth function $g(x,y)$

modeling size at t+1 as a (truncated) normal distribution with mean μ_y and standard deviation σ_y, x being the size at t

$$g(x,y) = dnorm(\boldsymbol{\mu}_y, \boldsymbol{\sigma}_y)$$

$$\mu_y = \beta_1 + \beta_2 x$$

$$\boldsymbol{\sigma}_y = f(x, \mathrm{cov}ariates, \ldots)$$ or constant

HOW TO IN R?: fit a linear model '**lm(y~x)**' in R to obtain the βs and σ_y and write the g(y,x) function.

Growth function *g(x,y)*

modeling size at t+1 as a (truncated) normal distribution
with mean μ_y and standard deviation σ_y, x being the size at t

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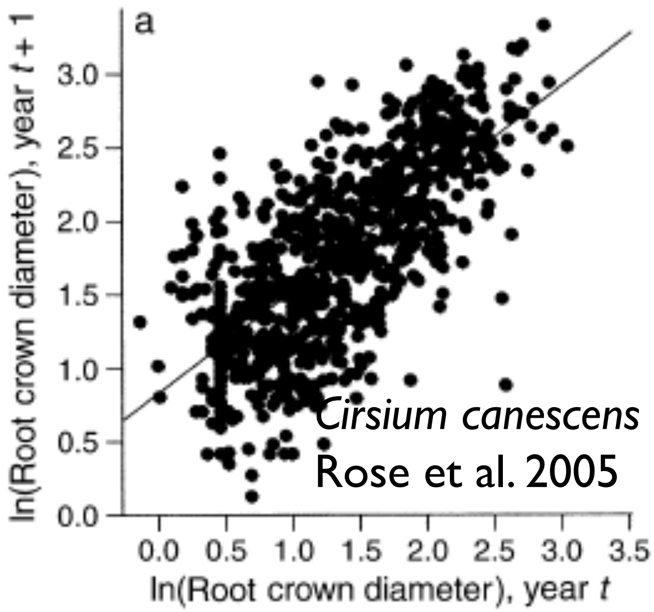
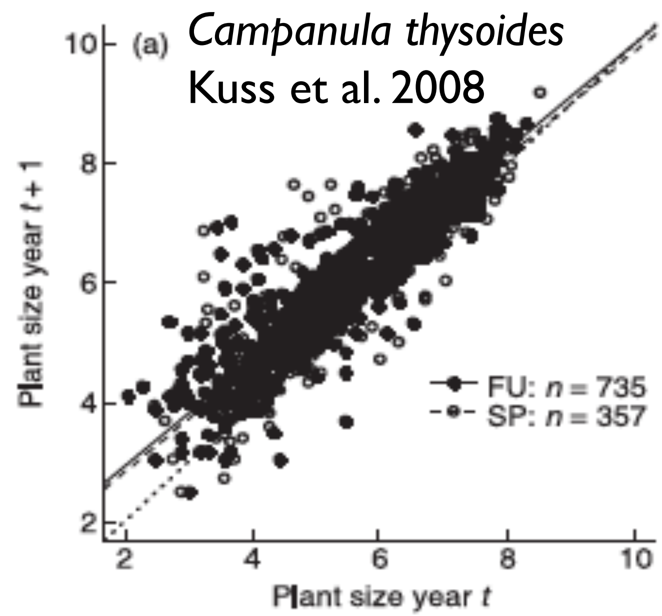
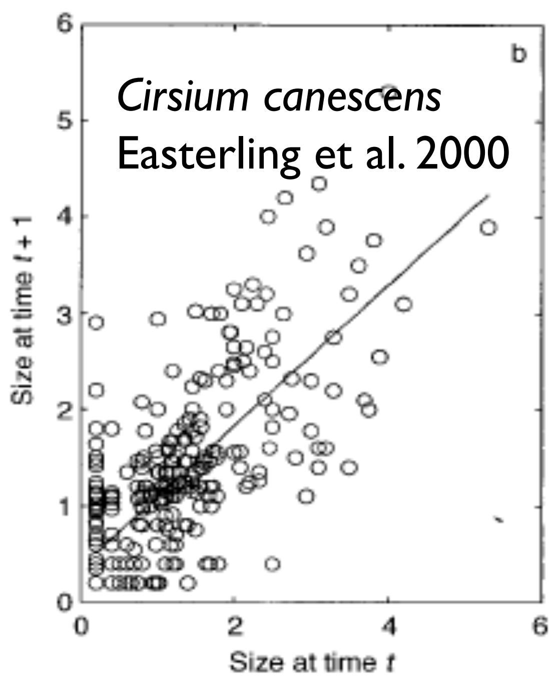
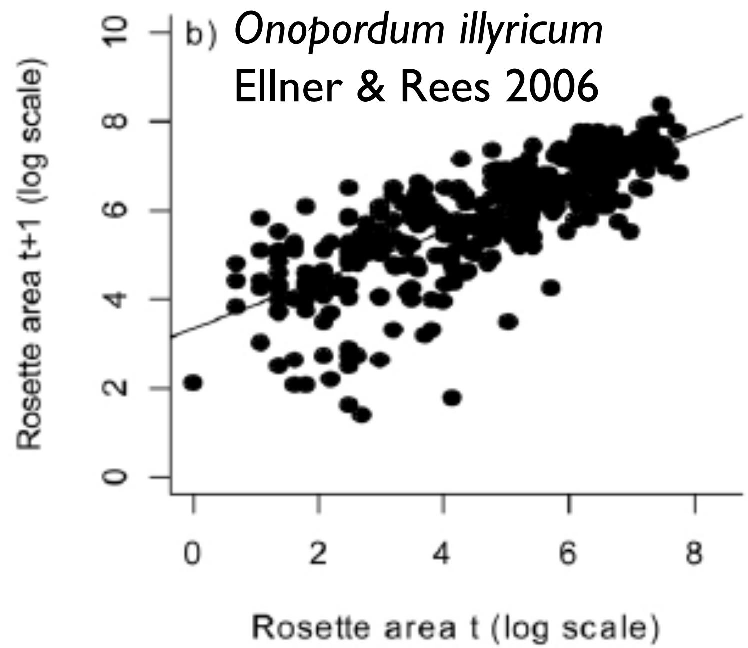

a
Cirsium canescens
Rose et al. 2005
ln(Root crown diameter), year t + 1
ln(Root crown diameter), year t


(a)
Campanula thysoides
Kuss et al. 2008
FU: n = 735
SP: n = 357
Plant size year t + 1
Plant size year t


b
Cirsium canescens
Easterling et al. 2000
Size at time t + 1
Size at time t


b)
Onopordum illyricum
Ellner & Rees 2006
Rosette area t+1 (log scale)
Rosette area t (log scale)

Size-dependent variance

Variance as a linear function of size

$$\sigma^2 = \Phi + \gamma \hat{y}$$

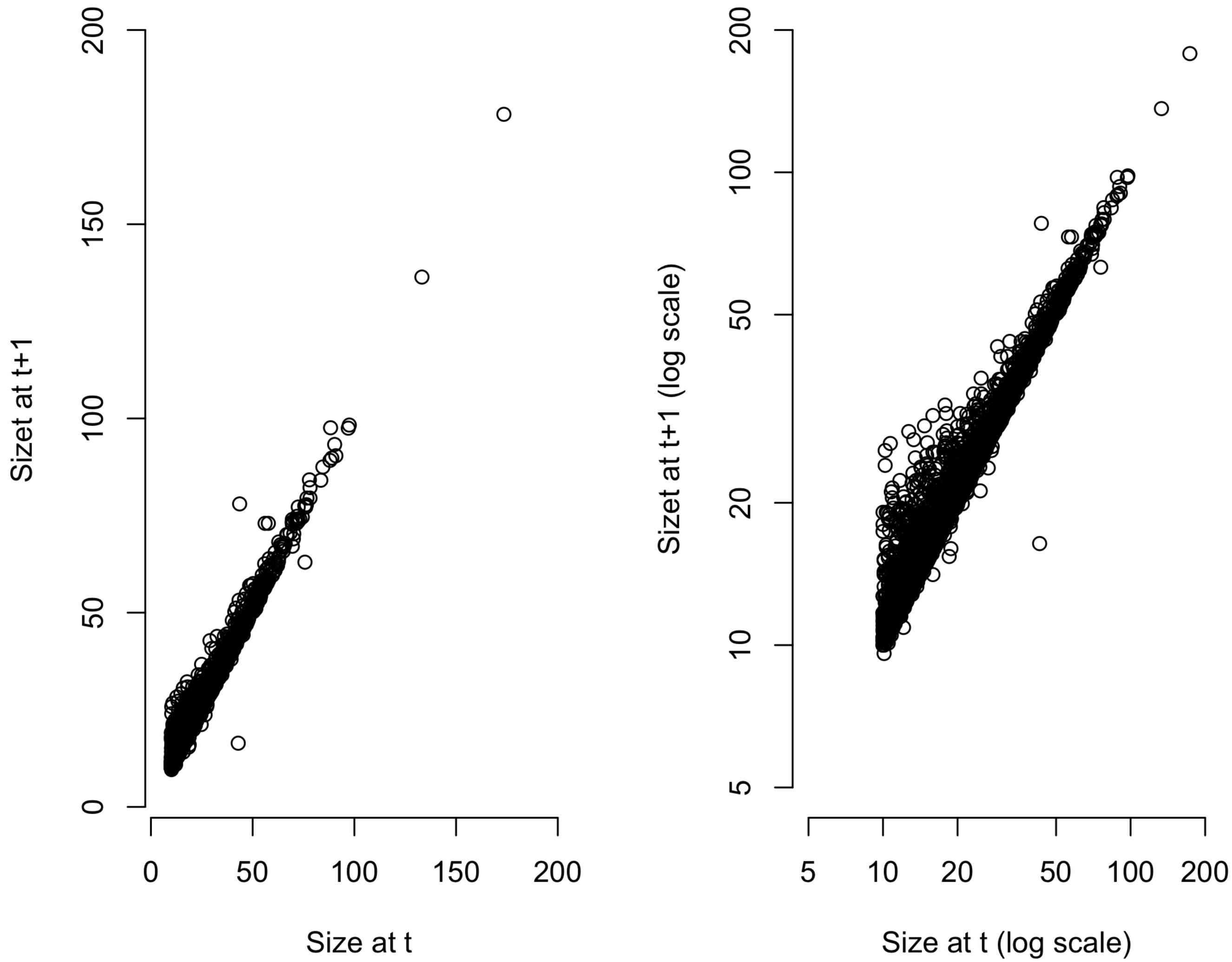
```
lm(var~x)
```

Exponential variance function (*varExp*)

$$\sigma^2 = \Phi \, exp(-\gamma \hat{y})$$

```
gls(s1~s0, weight=varExp(form=~fitted(.)))
```

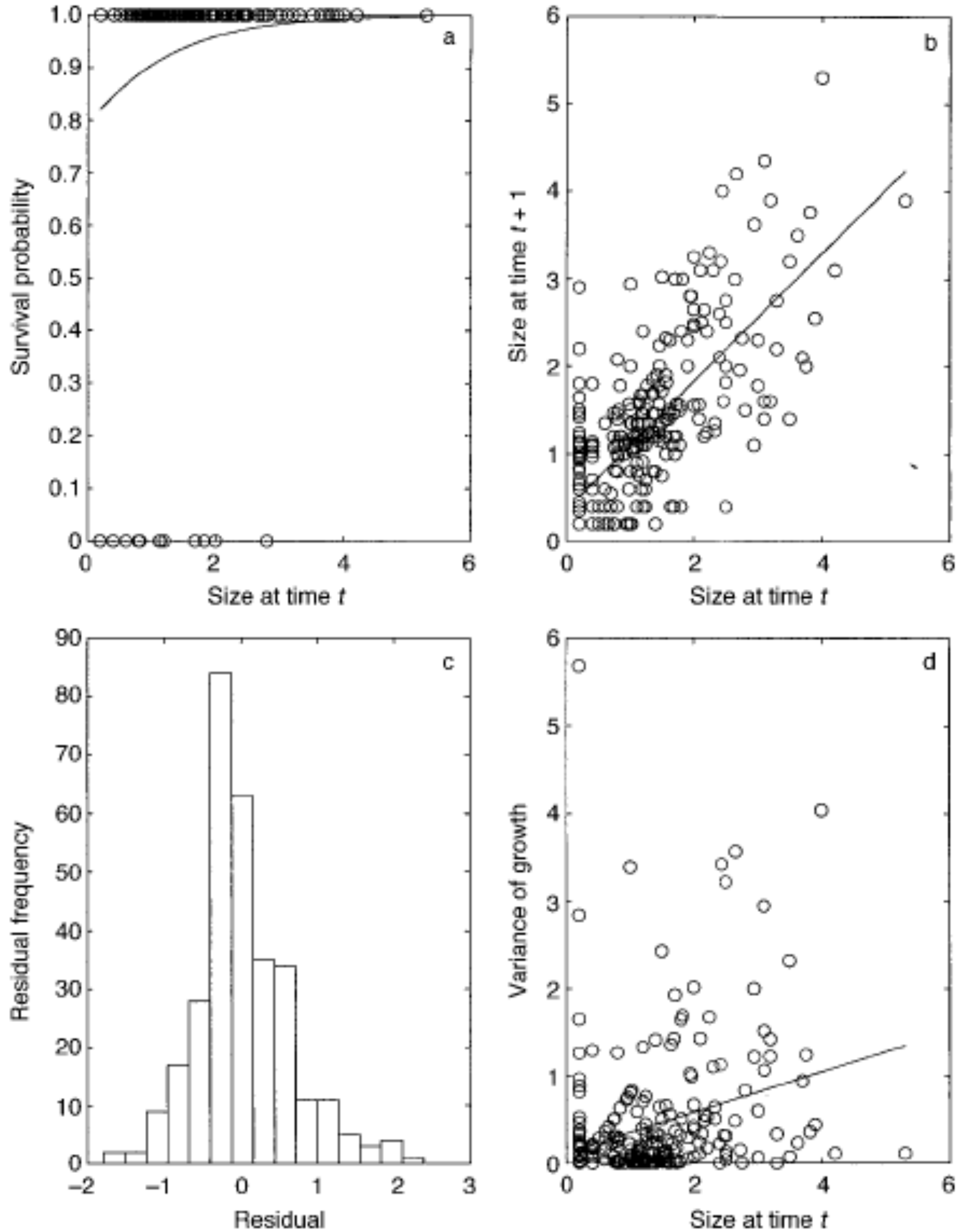
Exponential variance



Other variance functions

`varExp`	exponential of a variance covariate.
`varPower`	power of a variance covariate.
`varIdent`	constant variance (s), to allow different variances according to the levels of a classification factor.
`varFixed`	fixed weights, determined by a variance covariate
`varComb`	combination of variance functions.

Survival - Growth



Easterling et al. (2000); Fig. 1

Fertility function $f(x,y)$

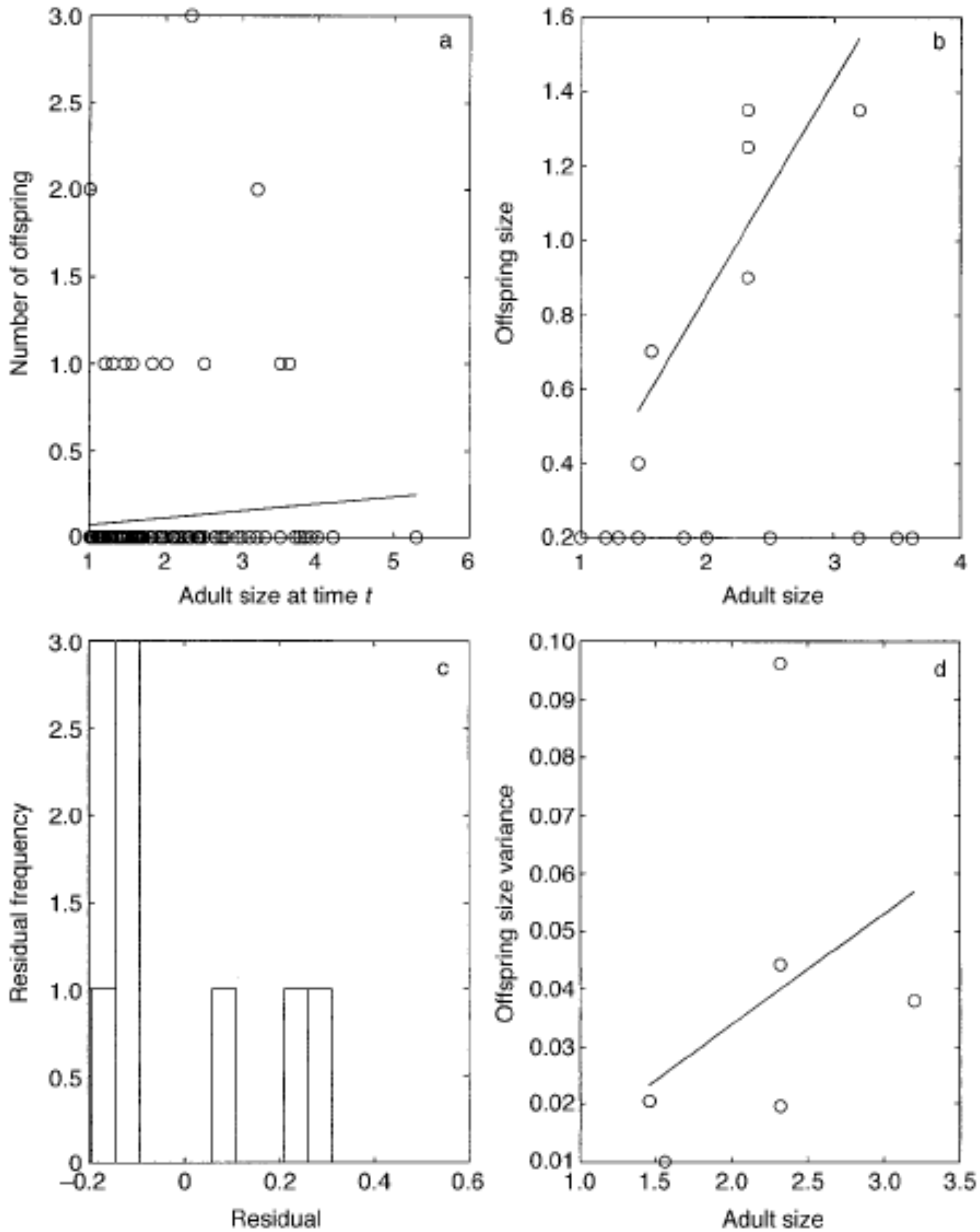
a combination of Poisson, logistic, normal distributions to obtain the size distribution of offspring.

$$f(x,y) = s(x) f_f(x) f_n(x) p_g p_e f_d(y)$$

$\boldsymbol{f_f(x)}$: $logit(y)=\beta_1+\beta_2 x$; probability of fruiting (logistic)
$\boldsymbol{f_n(x)}$: $log(\mu_f)= \beta_1+\beta_2 x$; number of fruits (*truncated* Poisson, negative binomial, zero-inflated Poisson)
$\boldsymbol{f_d(y)}$: $dnorm(\mu_{sdl},\sigma_{sdl})$: size distribution of seedlings (Normal)
$\boldsymbol{p_g}$: probability of seed germinating (field experiment)
$\boldsymbol{p_e}$: probability of seedling establishment (field, experiment).

HOW TO IN R?: fit a logisic **glm(y~x, binomial)**, Poisson model **glm(y~x, Poisson)**, to obtain the βs, calculate μ_{sdl}, σ_{sdl} from data, build function ***dnorm*** and write the f(x,y) function.

Fertility

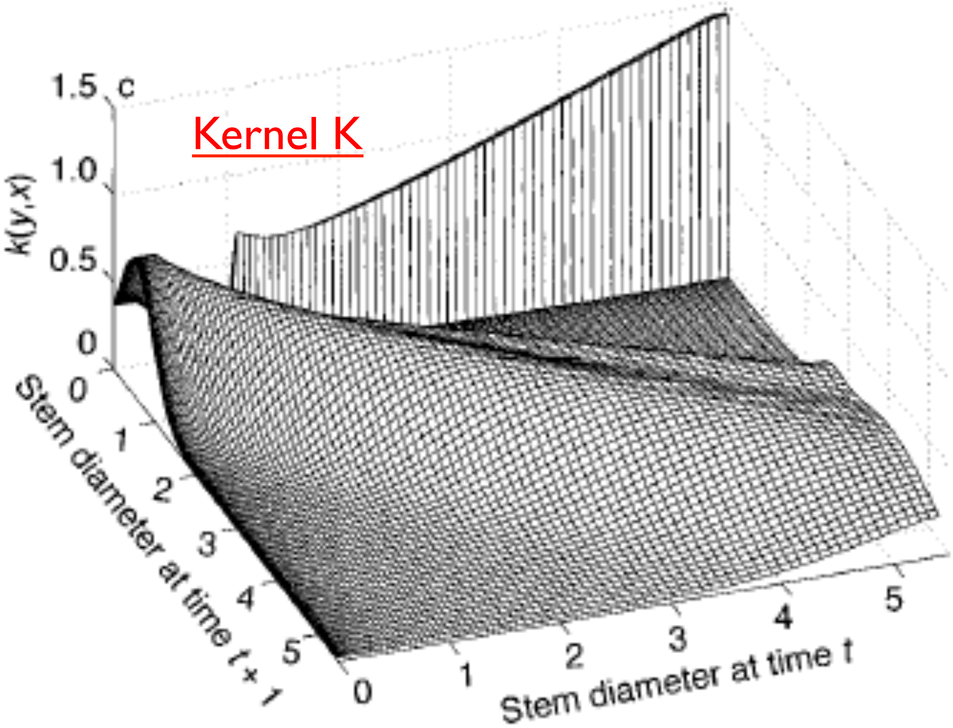


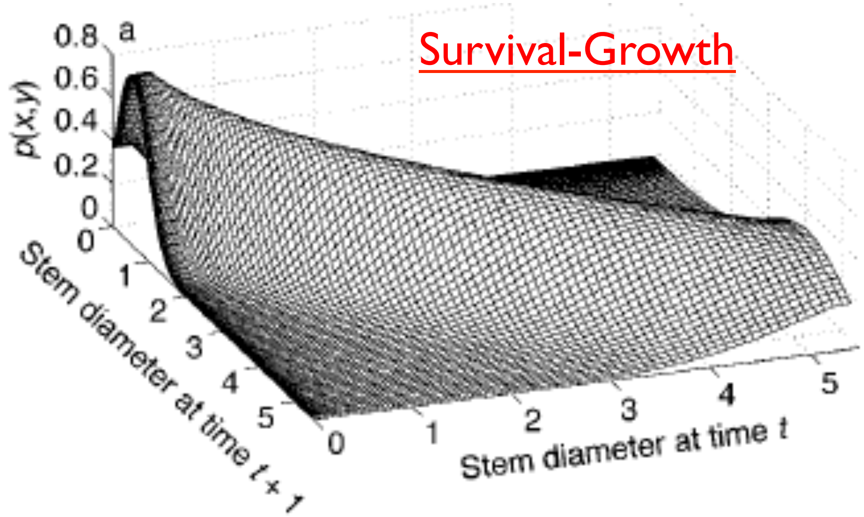
Easterling et al. (2000); Fig. 2

Step-by-step IPM

1. Fit statistical models to obtain the parameters for $s(x)$, $g(x,y)$ and $f(x,y)$
2. Write R functions for $s(x)$, $g(x,y)$ and $f(x,y)$ and
3. Combine functions to write the **Kernel** $K(x,y)=s(x)g(x,y)+f(x,y)$ as R function
4. Numerical integration of $K(x,y)$ by creating a "**big matrix**" (mid-point rule, integration,…)
5. Use basic matrix algebra to get the dominant eigenvalue, eigenvectors, and sensitivity analysis, LTRE ("`popbio`")

Kernel surface plot





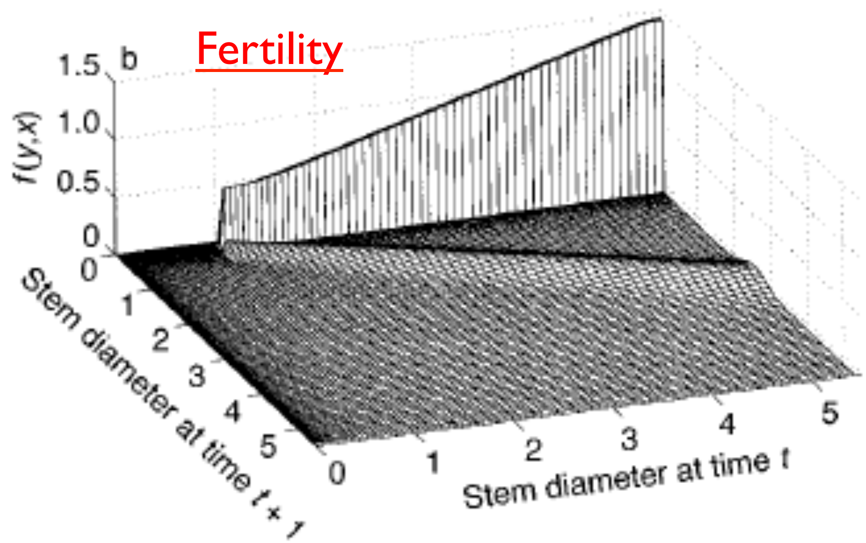
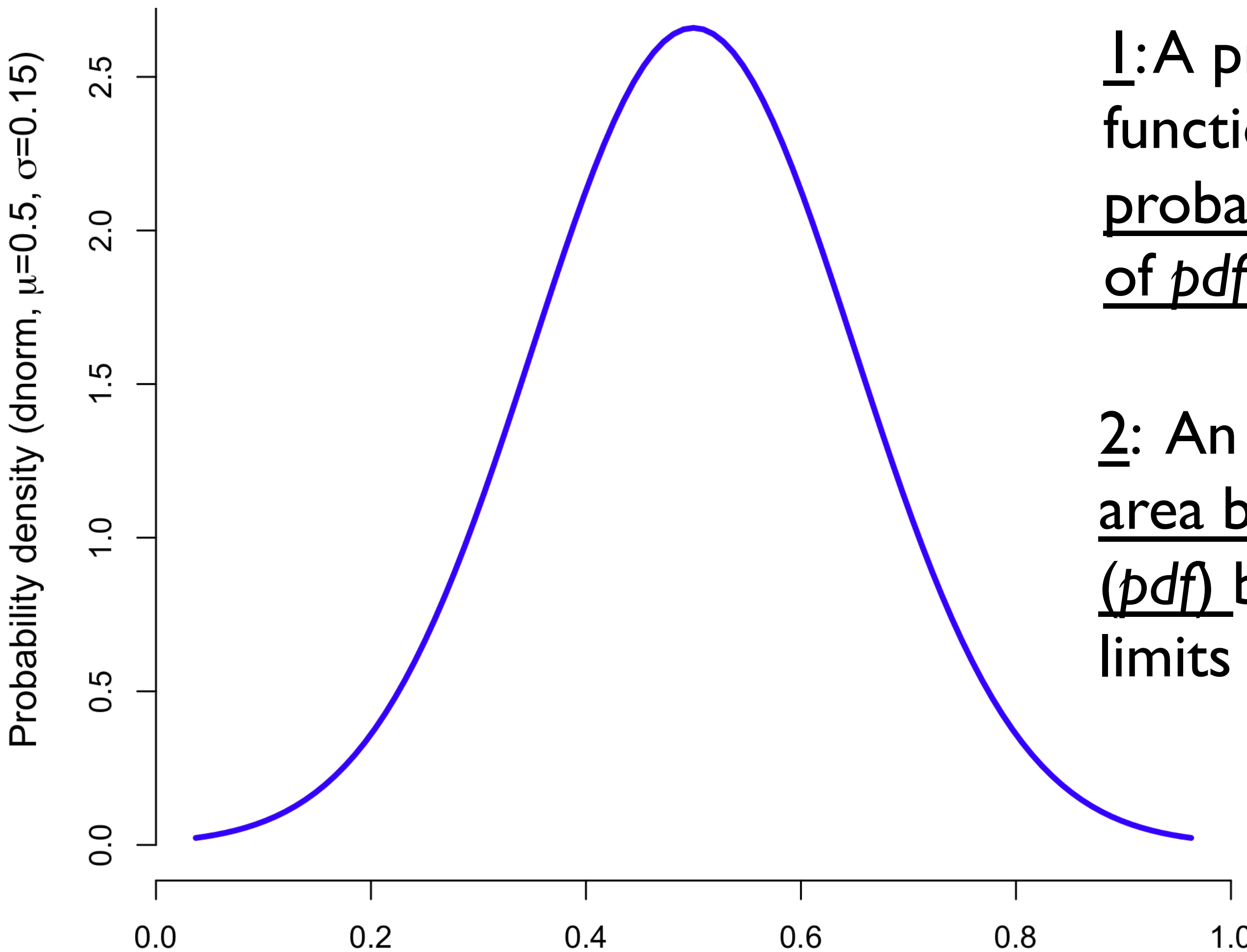


FIG. 3. The fitted kernel for monkshood and its components. (a) The survival function p. (b) The fecundity function f. (c) The kernel k. In the plot of the kernel, the curvature in the fecundity function's "ridge" results from the summation of small individuals' survival and fecundity, both of which produce small individuals.

Easterling et al. (2000); Fig. 3

Numerical integration

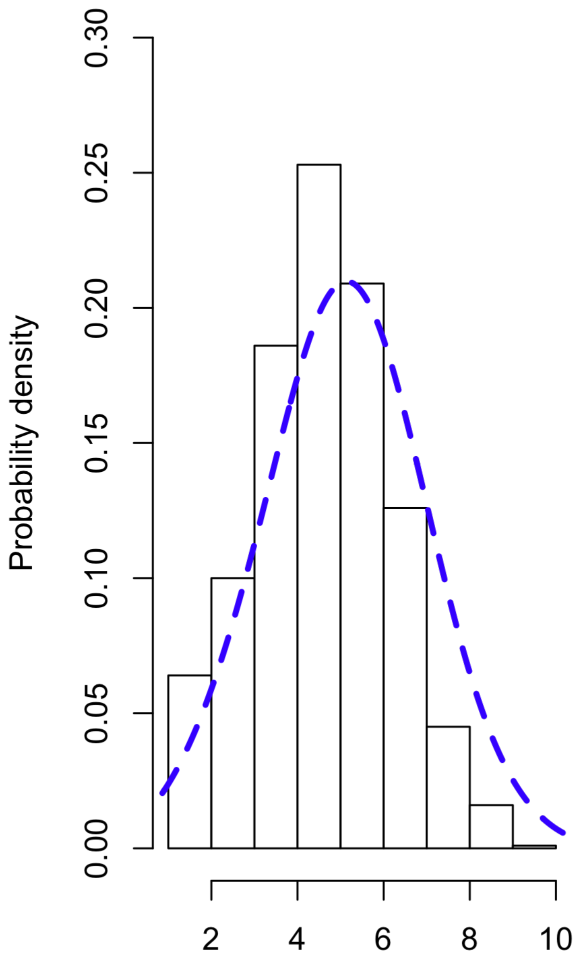


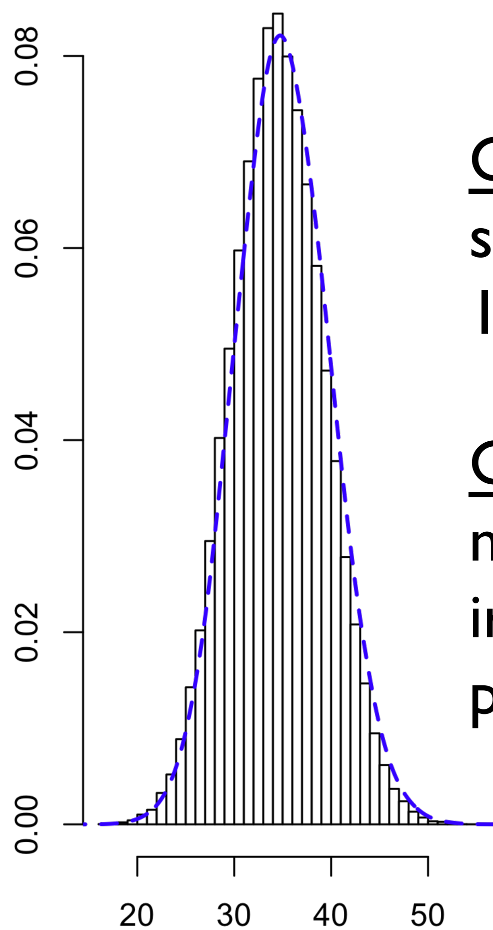
1: A probability density function (*pdf*) is not a probability; the integral of *pdf* is!

2: An integral is the area below the curve (*pdf*) bound by the limits of the integral

size of the "big matrix"

50 x 50 or 100 x 100 or 300 x 300…?

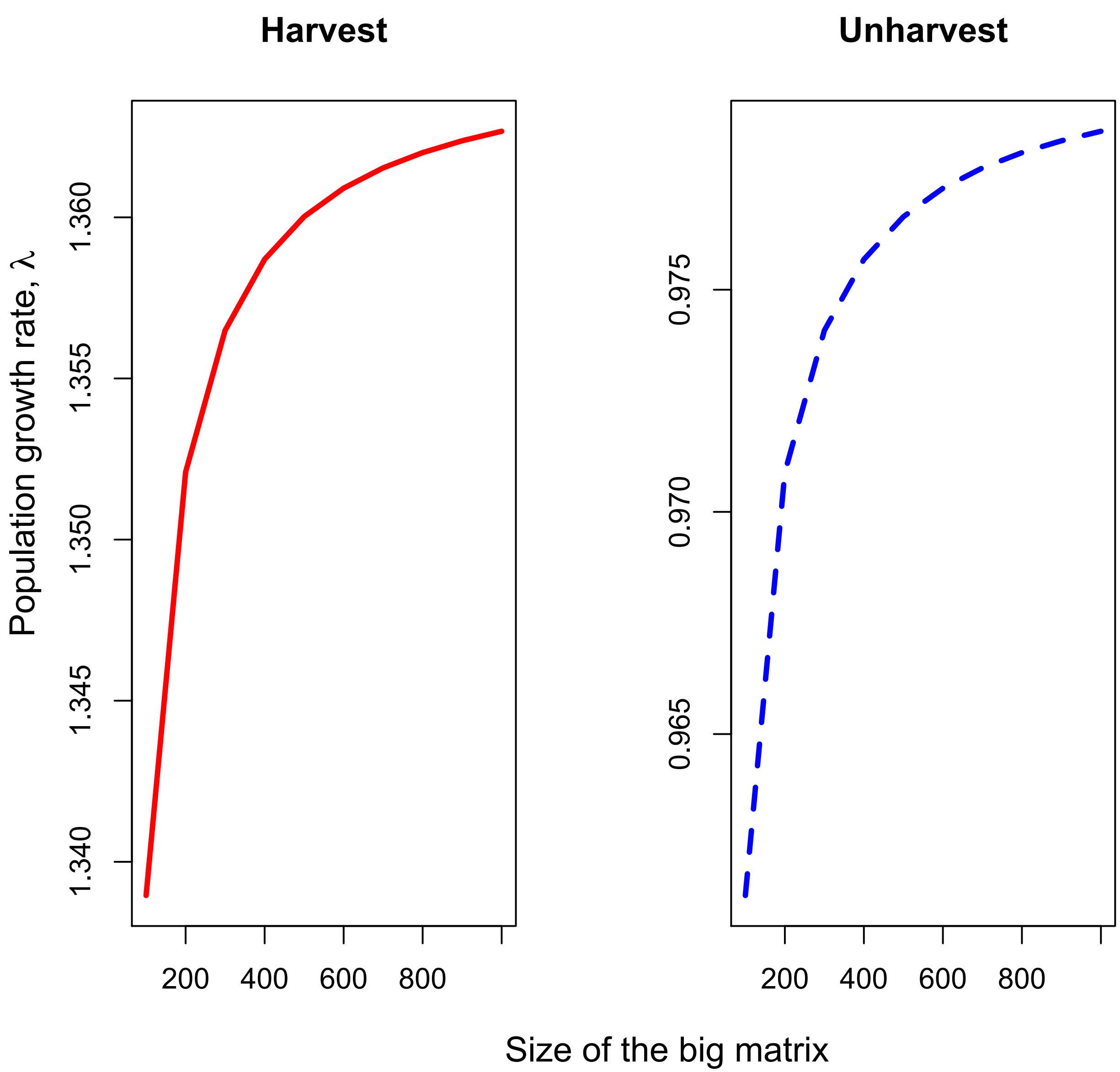




Check 1: Are the column sums of the big matrix =< 1?

Check 2: Is the big matrix non-negative and irreducible $(I+M_{sxs})^{s-1}$ is positive?

What size for the big matrix?



Findings eigenvalues and eigenvectors in R

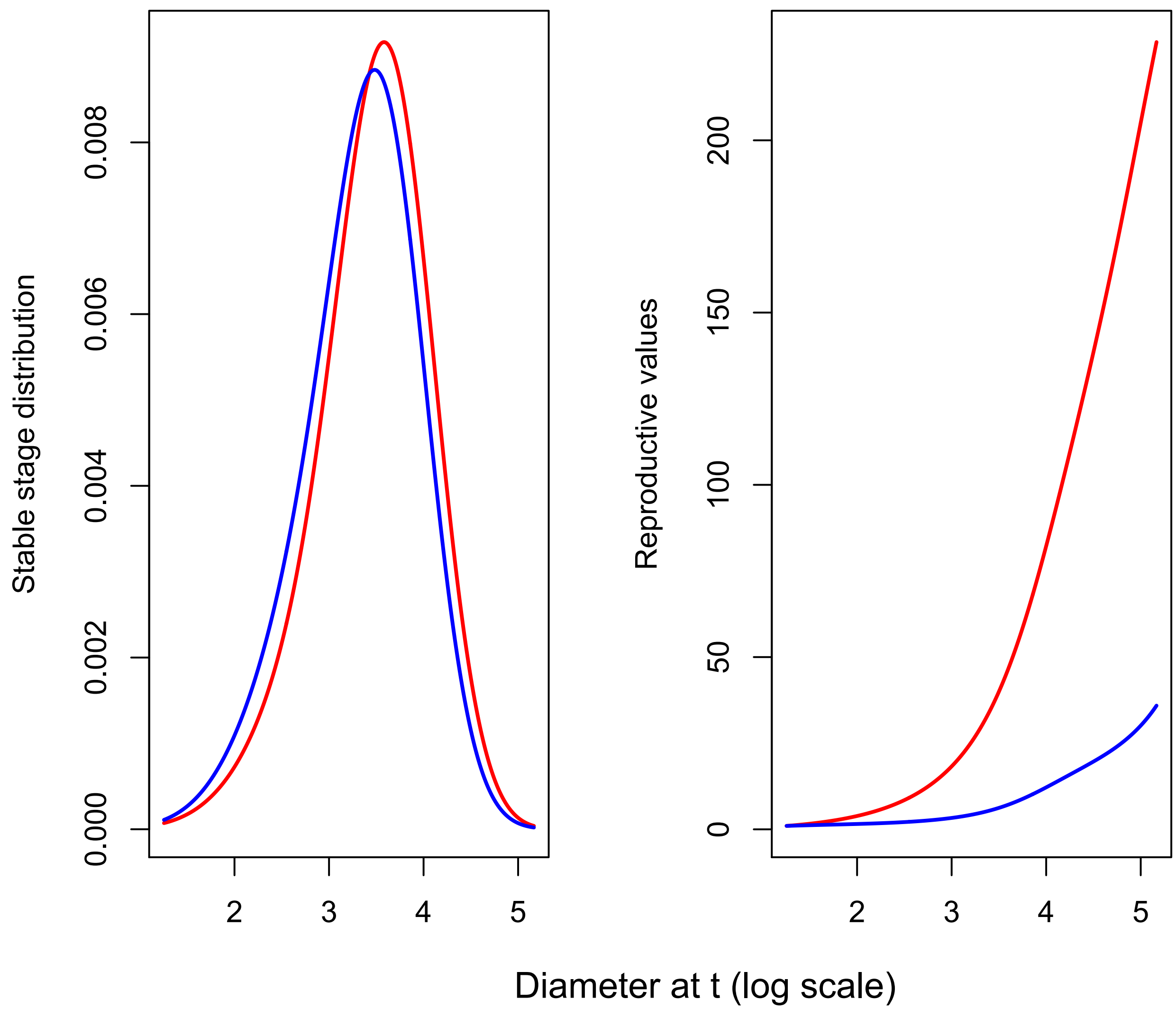
Let's M be the big matrix

```
e<-eigen(M)                 # eigenanalysis
lambda<-Re(e$values[1])     # dominant eigenvalue

## right eigenvector
w<-Re(e$vectors[,1])        # stable (st)age distribution
w<-v/sum(v)                 # standardize to total density

## left eigenvector
et<- eigen(t(M)
v<- Re(et$vectors[,1])
v<-w/w[1]                   # reproductive value
```

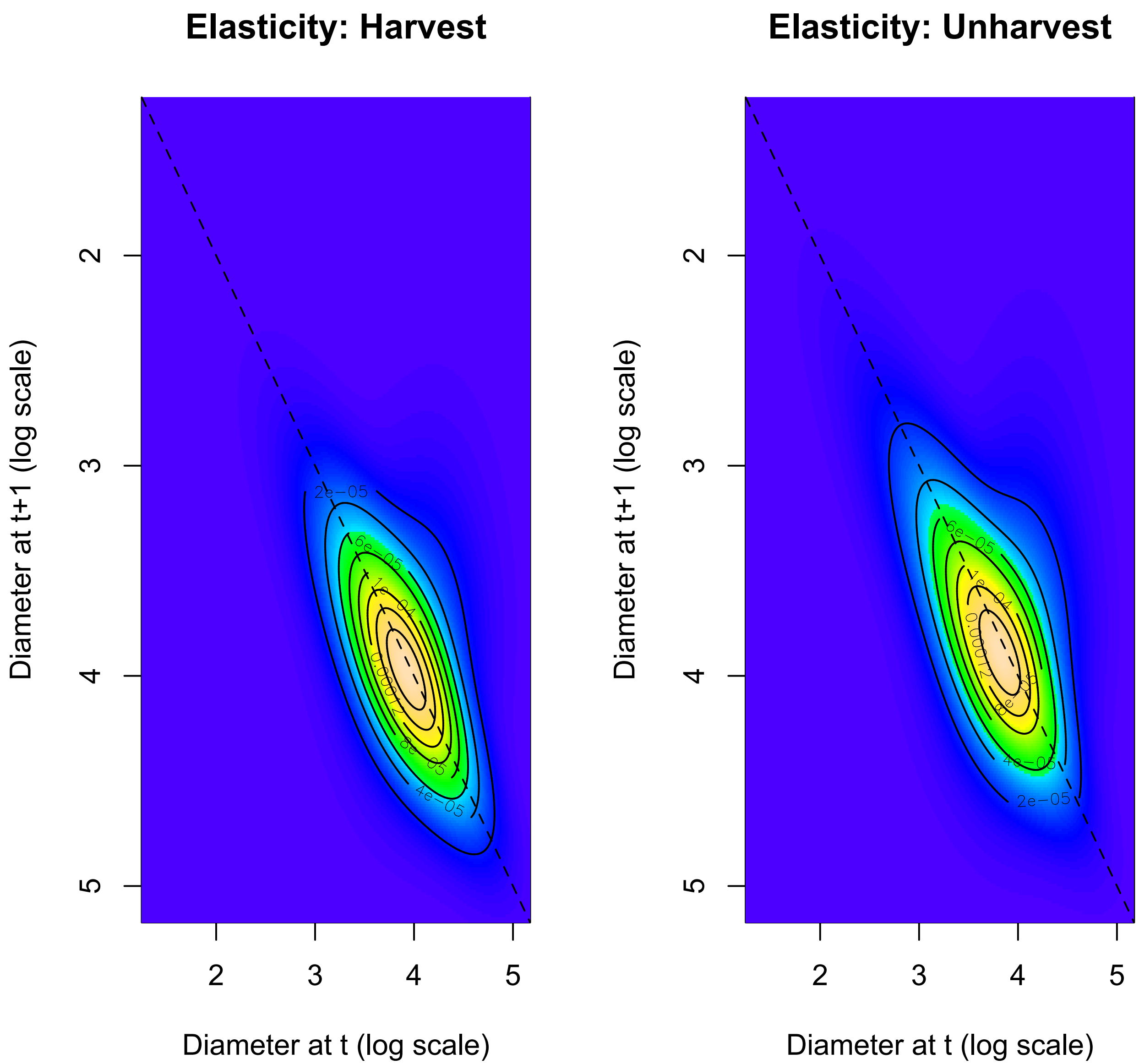
popbio

demogR

Stable stage distribution and Reproductive value



Elasticity analysis



IPM: what for?

- Estimate of age-specific demography parameters
  - age (not stage) at first reproduction
  - age of tropical trees
- Testing effect of multiple continuous factors on population dynamics
  - multiple NTFP harvest (foliage and bark, …)
  - NTFP harvest and variation in soil contents/rainfall
  - contribution of various reproductive strategies in variable ecological conditions
- Evolution of life histories strategies

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